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Managed and natural inundation: benefits for conservation of native fish in a semi-arid wetland system

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ABSTRACT

1. Floodplain wetlands are areas of high biodiversity and conservation value, including those in semi-arid regions. River regulation has resulted in disconnection from the main river channel of several ephemeral wetland systems, with profound modifications to their natural wetting/drying cycles that have contributed to the decline in diversity, distribution and abundance of native fish.

2. From 2005 to 2011, a series of managed inundation events through pumping followed by natural inundation allowed assessment and comparison of the fish assemblage developing in Hattah Lakes, a semi-arid wetland system of the regulated Murray River (Victoria, Australia).

3. As a result of one-way pumping from the main channel to Hattah Lakes, a 'filtered' fish assemblage consisting mainly of small-bodied native species and very low numbers of non-native species fully developed within 2 years. After disconnection from the main river channel in the absence of pumping, within-system recruitment also occurred, but later drying of all water bodies caused the entire fish assemblage to perish. Conversely, following two-way flooding by natural inundation a more diverse fish assemblage developed, including large-bodied native species but also non-native species, some of which were previously unrecorded.

4. Managed inundation through pumping in Hattah Lakes represents a viable option for the creation of fish habitat, for promoting recruitment, and as a measure of rehabilitation. However, the absence of connectivity back to the main river channel means that future measures should be implemented to maintain a refuge water pool until the next inundation event. Long-term monitoring is a key component of the integrated wetland conservation framework adopted by the Ramsar Wetland Convention, and this is especially relevant to the conservation of semi-arid wetlands world-wide including Hattah Lakes.
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KEY WORDS: Murray–Darling basin; Hattah Lakes; pumping; The Living Murray

INTRODUCTION

Floodplains are among the most dynamic ecosystems on Earth (Power *et al.*, 1995; Bunn and Arthington, 2002). They are highly complex, disturbance-dominated systems, defined as the river channel coupled with adjacent low-lying areas of land periodically inundated by the overflow of water from the river (Junk and Wantzen, 2004). The flow dynamics of floodplain rivers in their natural state has determined the shape and distribution patterns of river channels

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together with the swamps, marshes and wetlands that define the floodplain (Thorp *et al.*, 2008). Floodplain wetlands are characterized by enormous spatial and temporal habitat heterogeneity associated with expansion and contraction (i.e. wetting/drying) of flow cycles (Kingsford, 2000; Gawne and Scholz, 2006), complex aquatic–terrestrial coupling and exchange (Robinson *et al.*, 2002), and high biodiversity (Arthington *et al.*, 2010).

Regulation by headwater dams, levees and weirs coupled with extraction of water for irrigation has resulted in the disconnection from the main river channel of several wetlands throughout the world (Mitsch and Gosselink, 2011). The same is true in the Murray-Darling Basin (MDB: south-eastern Australia), where an estimated 90% of floodplain wetlands with varying degrees of hydrological permanence (Kingsford, 2000) have been detrimentally affected by river regulation, causing declines in the diversity, distributional range and abundance of freshwater fish (MDBC, 2003). Also, wetlands in the southern arid to semi-arid areas of the MDB have recently been subjected to additional stress by prolonged drought conditions (Murphy and Timbal, 2008), and climate change predictions indicate likely reductions of inflows into the southern MDB (CSIRO, 2008).

In regulated river systems like the Murray River, the return to a more natural flow regime through the delivery of 'environmental flows' is thought to provide an opportunity for ecosystem recovery and restoration (Arthington *et al.*, 2006). Environmental flows aim to restore key components of a river's natural flow regime to enhance ecosystem processes (Bunn and Arthington, 2002), and are often prescribed to reach specific restoration targets, such as maintenance of riparian woodlands or enhancement of fish and waterbird breeding (King *et al.*, 2010). Among the various modes of environmental flow delivery to wetlands, pumping water directly from the river channel is a relatively well documented option for restoration in man-made water bodies (Mitsch *et al.*, 1998, 2005). However, little is known of the influence of pumping water on the establishment of native fish assemblages in large-scale wetland systems. This is in contrast to recent large-scale intervention measures involving 'gravity-delivered' environmental water from the main river channel (King *et al.*, 2009, 2010).

To fill this gap, the present study examines the influence of managed inundation by (one-way) pumping on development of a fish assemblage in Hattah Lakes, a semi-arid wetland system (Williams, 1999) of high conservation value in the Murray River, and compares the outcomes with the fish assemblage resulting from a natural (two-way) inundation event. Spatial and temporal changes in fish population abundance, species richness, assemblage structure and recruitment (defined as the survival of a cohort to the end of the first year of life) are described, and the following hypotheses are made: (1) managed inundation through pumping will act as a 'filter' by preventing access of large-sized fish to Hattah Lakes, unlike natural inundation through overbank flooding; (2) the abundance and richness of both native and non-native fish species will be higher as a result of natural inundation compared with managed inundation owing to increased connectivity with the river channel; and (3) within-system spawning and recruitment will probably occur at least for some small-bodied (and short-lived) species in the absence of connection to the main channel. Benefits and limitations of hydraulic intervention for conservation of native fish are also discussed in the light of rehabilitation and restoration efforts within the constraints of river regulation.

STUDY AREA

Hattah Lakes is a semi-arid wetland system located in the Hattah–Kulkyne National Park, which covers ≈ 48 000 ha of the Murray River floodplain in the north west of Victoria, south-eastern Australia (34°41′14″S 142°22′54″E) (Figure 1). The park is part of the network of international Biosphere Reserves coordinated by the UNESCO Man and the Biosphere Programme, is classed as Category II (National Parks) in the IUCN List of National Parks and Protected Areas, and is managed primarily for ecosystem conservation and appropriate recreation (MDBC, 2005). Hattah Lakes includes more than 20 semi-permanent wetlands (12 of which are Ramsar-listed) connected by a series of floodplain channels and inundated by the Murray River during periods of moderately high flows. This mosaic of (mainly) ephemeral water bodies, consisting of shallow lakes (0.4–2.8 m retained water depth) and anabranches, provides important breeding habitat for a range of biota in an otherwise semi-arid landscape receiving an annual average rainfall of ≈ 250 mm (cf. Williams, 1999). Hattah Lakes also supplies water essential for maintaining healthy riverine woodlands (mainly river red gum *Eucalyptus camaldulensis*) fringing the many water bodies; whereas during dry phases, lake beds and fringing areas provide critical habitat for terrestrial birds, mammals and reptiles, and act as 'seed banks' for macrophytes and aquatic invertebrates (MDBC, 2005).

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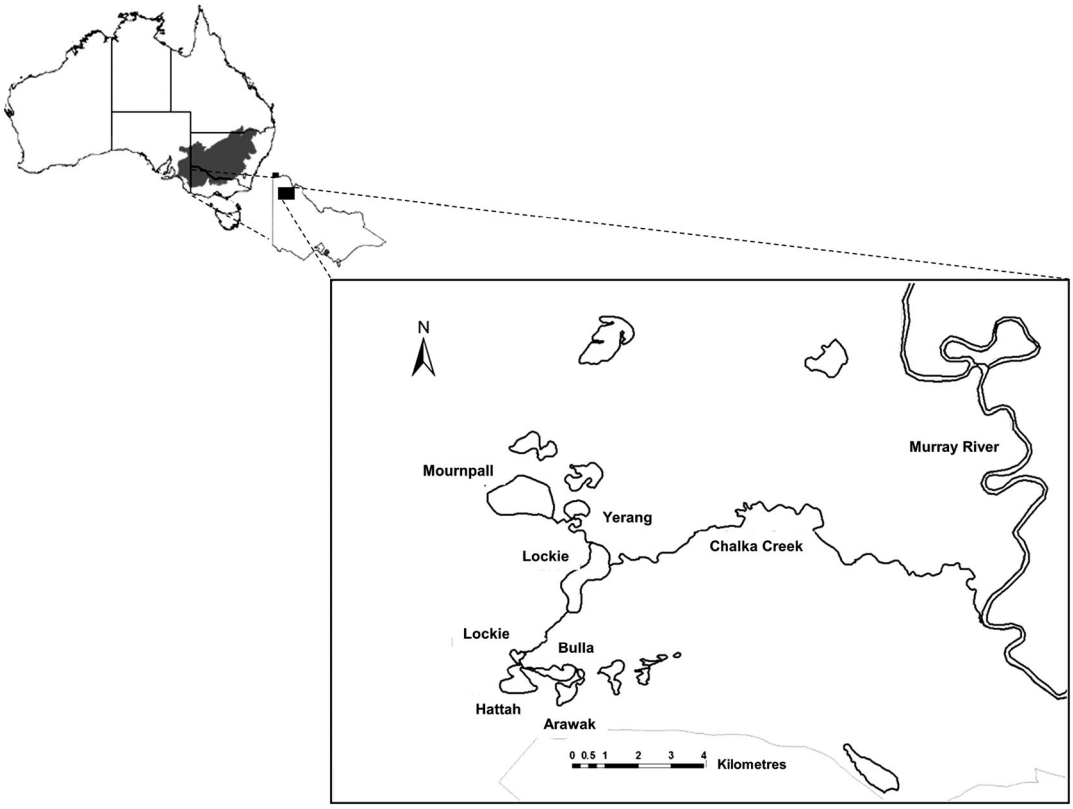

Figure 1. Study area showing the water bodies of the Hattah Lakes wetland system (south-eastern Australia, Victoria) sampled for fish from 2005 to 2011. Shaded area of Australia represents the Murray–Darling Basin.

River regulation has threatened the ecological values of Hattah Lakes, with storage and extraction from the Murray River upstream of the system reducing discharge to $\approx 50\%$ of natural levels (Maheshwari *et al.*, 1993) (Figure 2(a)). The combined effects of these changes, along with historical modifications of Hattah Lakes (Souter, 2005), have been: (i) a reduction in flooding frequency and duration by 57% and 65%, respectively; and (ii) a delay in the timing of flooding from August to September/October (MDBC, 2005). As a result, while under natural conditions the majority of water bodies would have been semi-permanent (*sensu* Williams, 2006), under current conditions of river regulation they now receive reduced inflows and are wet for shorter periods. By way of example, for the period 1996–2010 under modelled natural conditions the wetland system would have received flood waters on at least seven occasions but, due to regulation, natural inundation occurred only once (Figure 2(b)).

As part of The Living Murray (TLM) initiative (http://www.mdba.gov.au/programs/tlm), one of Australia's most significant restoration programmes, the conservation objectives for Hattah Lakes have been four-fold: (1) restore a mosaic of healthy wetland and floodplain communities to maintain the ecological character of this Ramsar site; (2) maintain high quality habitat for native fish in wetlands and support successful breeding events; (3) provide feeding and breeding habitat for a range of waterbird species; and (4) provide conditions for successful breeding of colonial nesters at least twice every 10 years.

MATERIAL AND METHODS

Pumping and monitoring

In response to the changed hydrology of Hattah Lakes and reductions in the condition of riparian woodlands and biodiversity, a strategy was developed as part of the TLM initiative to return water to the system by pumping water from the Murray River channel. Since 2005, managed inundation of some water bodies in the Hattah Lakes system has been achieved by pumping using a combination of free-standing, truck- and trailer-mounted, impeller-type pumps, each delivering 1.0–2.5 ML h^{-1} and with the

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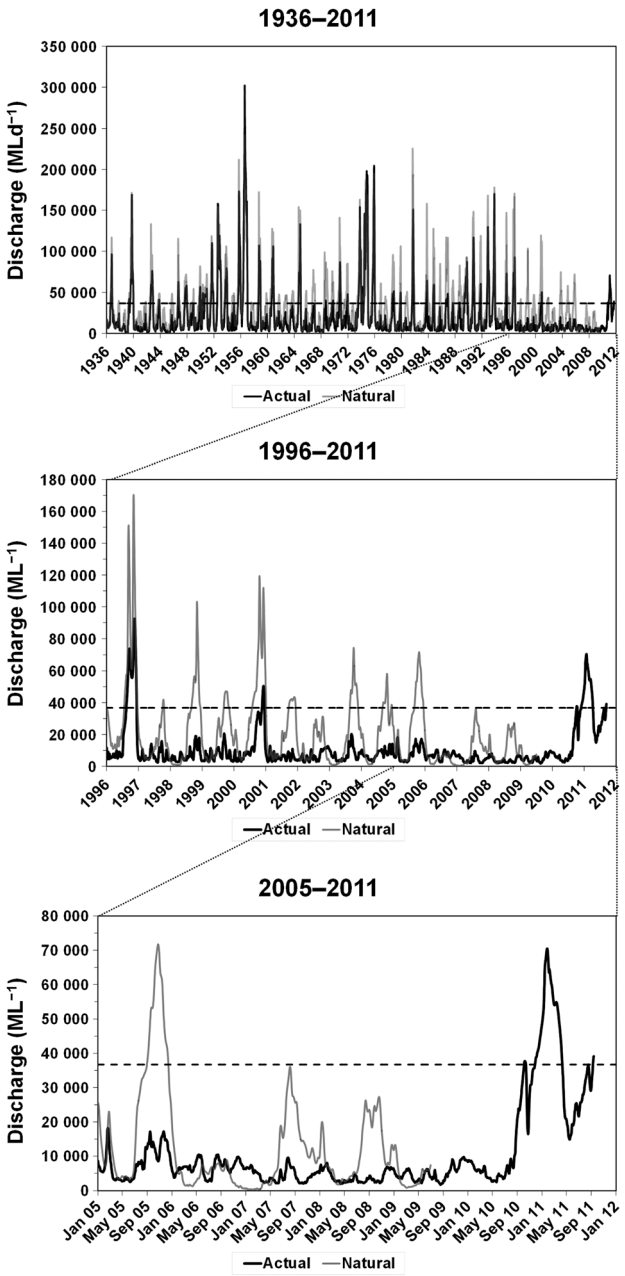

Figure 2. Actual (black line) and modelled natural (grey line) discharge at Euston (≈70 river km upstream of Hattah Lakes) for: (a) the historical reference period; (b) the last 15 years; and (c) the present study period. Dashed line indicates the 36 700 ML day^{-1} commence-to-fill-threshold (CTFT: Souter, 2005) for inflows into Hattah Lakes.

off-take located >10 m from the bank and at a depth >1 m. To prevent the uptake of material (including large fish) from the River Murray into pumps, screens with circular perforations of a maximum 75 mm and 100 mm diameters were located on the pump off-takes for pumping events I–VI and VII, respectively. These intervention measures have been paralleled by regular, long-term monitoring of the biota in the wetland system.

Fish sampling

To evaluate Conservation Objective 2, 10 fish sampling events occurred between April 2005 and March 2011, with up to eight water bodies surveyed at any one time depending upon surface water availability and logistic constraints (Figure 3). An adjacent reach of the Murray River (Figure 1), the source of water and fish for both managed and natural inundation, was also sampled concomitantly (five events in total) to compare the riverine fish assemblage with that of Hattah Lakes. For each water body of Hattah Lakes and in the Murray River, three sites were repeatedly sampled on each event. Notably, sampling events were a combination of 'condition' (events 1–3, 5 and 7–10) and 'intervention' monitoring (events 4, 6, and 7), the former being surveillance-oriented (*sensu* Finlayson, 2003) and the latter hypothesis-driven to investigate the response of the wetland system to the first series of pumping events (i.e. first managed inundation period).

At Hattah Lakes, for all 10 sampling events large and small fyke nets were set in the afternoon and retrieved the next day at depths of 0.4–0.8 m, depending on water availability. Large fyke nets (32 mm stretched mesh) consisted of a central wing (8 m × 0.65 m) attached to the centre of the first of seven supporting hoops (Ø = 0.55 m), and were placed perpendicular to the shoreline; small fyke nets (2 mm stretched mesh) consisted of dual wings (2.5 m × 1.2 m each) with three supporting hoops (Ø = 0.55 m) and a rigid plastic grid (0.5 m × 0.5 m) to exclude larger fish and turtles, and were placed parallel to the shoreline. In the Murray River, for a total of five sampling events boat electrofishing (Pulsed DC 4800–5000 W, 120–350 V, 60–120 Hz) was employed at each site with each shot covering ≈ 300–400 m of channel length (Table 1).

In addition to regular sampling, at Hattah Lakes backpack electrofishing (Smith-Root™ LR 24 Backpack Electrofisher), unbaited concertina bait traps and a seine net sweep (5 m × 1.5 m, 5 mm stretched mesh and fitted with a cod-end, and hauled in an arc of 180° spanning from the bank for 5–10 m) were also used later in the study period, and on one sampling event gill nets (20 m × 2 m with panels of 6.5 cm, 10 cm and 15 cm stretched mesh) were deployed in lakes Hattah and Mournpall (the two deeper water bodies that still contained ≈ 0.5 m maximum water depth) to investigate the occurrence of large-bodied fish (>300 mm) that were not

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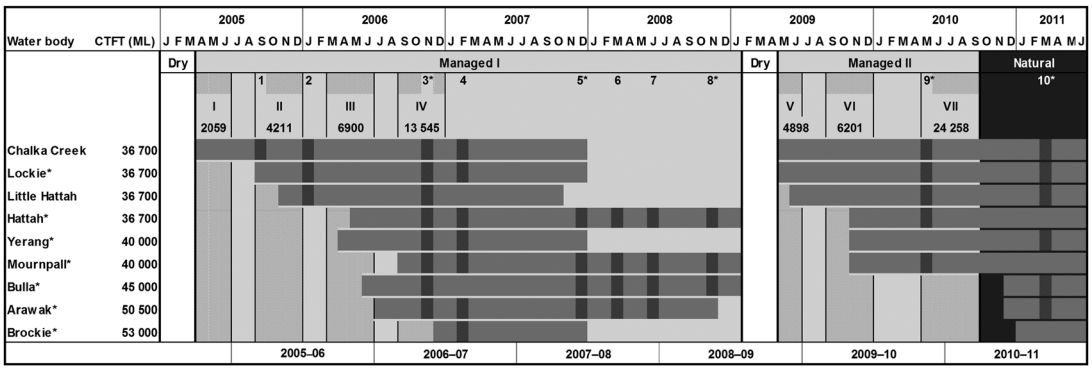

Figure 3. Summary timeline of the inundation events at Hattah Lakes from 2005 to 2011 (fish breeding seasons below). For each water body (Ramsar-listed marked by an asterisk) sampled for fish, CTFT is provided. Dry, managed inundation through pumping and natural inundation periods highlighted (white, grey and black background, respectively) along with duration of inundation for each water body (dark grey bars). Arabic (1–9) and Roman numerals (I–VII) indicate sampling events (underlined for intervention monitoring, otherwise for condition monitoring; asterisk includes the adjacent Murray River) and pumping events (with duration marked by a dotted area along with ML of water delivered), respectively. Sampling in each water body marked by diagonal stripes.

collected with other techniques but were anecdotally reported as being present. In the Murray River, later in the study period small fyke nets, bait traps and seine hauls were also used (Table 1).

All fish were identified to species (McDowall, 1996; Allen *et al*., 2002; Lintermans, 2007), except for the 'carp gudgeon complex' *Hypseleotris* spp. of uncertain taxonomy (Bertozzi *et al*., 2000), and counted. The standard length (SL) of the first 15–50 individuals of each species sampled with each small fyke net and bait trap was measured to the nearest 1 mm; all fish from large fyke nets, gill nets and (boat/backpack) electrofishing were measured for length and weighed to the nearest 1 g. Native fish were returned alive to the water at the point of capture, whereas non-native fish were euthanized as per ethics requirements. By convention, distinction between large- and small-bodied species is based on the latter rarely exceeding a maximum SL of 100 mm (Table 2; Lintermans, 2007).

Data analysis

Owing to the different sampling methods used throughout the study period (cf. Table 1), all comparisons of fish abundance were standardized as catch-per-unit-effort (CPUE: fish h^{-1}) based on the methods consistently used across sampling events. Accordingly, at Hattah Lakes CPUE abundance was computed as number of fish per hour sampled with large and small fyke nets, and in the Murray River as number of fish per hour sampled by boat electrofishing. Conversely, comparisons of frequency of occurrence, presence/absence and richness both at Hattah Lakes and in the Murray River were based on the total (raw) number of fish collected with all sampling methods (Table 1).

To test Hypotheses 1 and 2, in Hattah Lakes fish abundance (large- and small-bodied species, and common carp separately) and richness (all, native

Table 1. Fish sampling methods used at Hattah Lakes and in the adjacent Murray River from 2005 to 2011. For electrofishing, replicates (per sampling site) refer to 'shots'. See also Figure 3

			Sampling event									
Method	Replicates	Time	1	2	3	4	5	6	7	8	9	10
Hattah Lakes												
Large fyke nets	2	≈15–26 h	√	√	√	√	√	√	√	√	√	√
Small fyke nets	2	≈15–26 h	√	√	√	√	√	√	√	√	√	√
Backpack electrofishing	8	150 s									√	√
Bait traps	10	≈2 h										√
Seine nets												√
Gill nets	2	≈2 h								√		
Murray River												
Boat electrofishing	12	90 s			√		√			√	√	√
Small fyke nets	2	≈15–26 h								√	√	√
Bait traps	10	≈2 h									√	√
Seine nets	1	–									√	√

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Table 2. Fish species collected from Hattah Lakes (HL) and the adjacent Murray River (MR) from 2005 to 2011, with indication of relative abundance and maximum standard length (SL) of young-of-year (YOY)

Species	Common name	Abbreviation	Relative abundance (%)			YOY max SL (mm)
			HL	MR	Total	
Native						
Large-bodied						
Bidyanus bidyanus	Silver perch	Bid.bid	0.01	0.02	0.01	100[1]
Leiopotherapon unicolor	Spangled perch	Lei.uni	< 0.01	–	< 0.01	65[2]
Macquaria ambigua	Golden perch	Mac.amb	0.17	0.34	0.20	100[1]
Maccullochella peelii peelii	Murray cod	Mac.pel	< 0.01	0.10	0.02	100[3]
Nematalosa erebi	Bony herring	Nem.ere	0.12	3.84	0.76	81[4]
Small-bodied						
Craterocephalus stercusmuscarum fulvus	Unspecked hardyhead	Cra.ste	2.62	4.35	2.92	41[2]
Hypseleotris spp.	Carp gudgeon	Hyp.spp	86.04	63.78	82.20	28.1[2]
Melanotaenia fluviatilis	Murray-Darling rainbowfish	Mel.flu	0.02	0.24	0.06	30.0[5]
Philypnodon grandiceps	Flathead gudgeon	Phi.gra	1.85	0.21	1.56	45.9[2]
Philypnodon macrostomus	Dwarf flathead gudgeon	Phi.mac	–	0.01	< 0.01	24.3[2]
Retropinna semoni	Australian smelt	Ret.sem	7.10	0.93	6.03	32.8[2]
Non-native						
Large-bodied						
Carassius auratus	Goldfish	Car.aur	0.42	0.21	0.38	86[6]
Cyprinus carpio carpio	Common carp	Cyp.car	1.19	0.80	1.12	148[7]
Cyprinus carpio × *Carassius auratus*	Common carp × goldfish	Cyp.hyb	< 0.01	–	< 0.01	117[7]
Misgurnus anguillicaudatus	Oriental weatherloach	Mis.ang	0.05	0.02	0.04	75[8]
Small-bodied						
Gambusia holbrooki	Eastern mosquitofish	Gam.hol	0.42	25.14	4.69	20.0[9]

[1]Mallen-Cooper and Stuart (2003); [2]Pusey *et al.* (2004); [3]Anderson *et al.* (1992); [4]Puckridge and Walker (1990); [5]www.fishbase.org; [6]Specziár *et al.* (1997); [7]Vilizzi (unpublished data); [8]Freyhof and Korte (2005); [9]Vargas and de Sostoa (1996).

and non-native species separately) were compared among inundation periods (i.e. Managed I, Managed II, Natural) at the site level during events 3 (Managed I), 9 (Managed II) and 10 (Natural) in Chalka Creek, Lockie and Little Hattah – the three water bodies retaining water (hence, being sampled) during the three inundation periods (Figure 3). Richness (= sum of species) was instead computed at the water body level. For both CPUE abundance and richness, statistical comparisons among inundation periods were made with univariate permutational analysis of variance (PERANOVA) following normalization and using a Euclidean distance, with statistically significant effects ($\alpha = 0.05$) followed by *a posteriori* pair-wise comparisons. Statistical analyses were carried out in PERMANOVA + v1.0.1 for PRIMER v6.1.11, with 9999 permutations of the raw data (Anderson *et al.*, 2008).

To test Hypothesis 3, within-system recruitment (at Hattah Lakes) was estimated from length–frequency distributions of the most abundant large-bodied (i.e. golden perch, goldfish and common carp) and small-bodied species (i.e. carp gudgeon, flathead gudgeon and Australian smelt) collected in the 2007–2008 and 2008–2009 fish 'breeding seasons' (taken to last from July to June based on spawning calendars for MDB fish: Vilizzi, 2011), when no pumping events occurred (Figure 3). To distinguish between young-of-year (YOY) and 1+ individuals, maximum size thresholds for YOY were obtained from published literature and, whenever necessary, converted to SL with species-specific factors as per www.fishbase.org and Pusey *et al.* (2004) (Table 2).

RESULTS

Flooding events

Before pumping in 2005, Hattah Lakes had been dry since 2002 (Figure 2(b)). A first managed inundation period, involving four pumping events, lasted from April 2005 to December 2008 and delivered 26 715 ML of environmental water in total (Figure 3). In September 2008, maximum water depth in the water bodies still inundated ranged from 0.2–0.5 m, and by February 2009 the entire wetland system had dried out. Hattah Lakes remained dry for a few months (i.e. February–April 2008) until a second managed inundation period occurred involving three pumping events from May 2009 to September 2010, delivering 35 357 ML (Figure 3). Natural inundation then occurred in October 2010, when

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Murray River discharge (gauged upstream at Euston weir) first exceeded for a few days the 36 700 ML d^{-1} commence-to-fill-threshold (CTFT), and then again from late November 2010 until mid-April 2011 with discharge peaking at 70 454 ML d^{-1} on 26 January 2011 (Figure 2(c)).

Abundance and richness

In total, 109 469 fish, with 90 556 from Hattah Lakes, were collected during the study period, comprising 11 native and five non-native species (including common carp × goldfish hybrids) (Table 2). Small-bodied species dominated the fish assemblage both at Hattah Lakes and in the adjacent Murray River, with carp gudgeon being by far the most abundant, followed by eastern mosquitofish (mainly in the Murray River), Australian smelt, unspecked hardyhead and flathead gudgeon. Common carp was the most abundant large-bodied species at Hattah Lakes, and second in abundance after bony herring in the Murray River. In addition, one spangled perch and two common carp × goldfish hybrids (in a ratio of about 2:1000 to common carp and 5:1000 to goldfish) were recorded only from Hattah Lakes, and one dwarf flathead gudgeon only from the Murray River.

In Hattah Lakes, during the first managed inundation period fish CPUE abundance (small and large fyke nets) increased progressively until February–December 2007 and decreased thereafter (Figure 4(a)), with carp gudgeon and Australian smelt being the most frequently occurring species (Figure 4(b)), after which the entire fish assemblage perished owing to the complete drying of the wetland system in February 2009. Following re-filling by pumping, in May 2010 species abundance was still low and not statistically different from that recorded in January 2006 after a similar time lapse since the beginning of inundation (PERANOVA: $F^{\#}_{1,14} = 0.22$; $P^{\#} = 0.651$) (Figure 4(a)), and Australian smelt was the most frequently encountered species followed by carp gudgeon (Figure 4(b)). In March 2011 during natural inundation, abundance increased sharply (Figure 4(a)) and carp gudgeon was again the most frequently encountered species (Figure 4(b)). Non-native oriental weatherloach and eastern mosquitofish were recorded only during natural and never during managed inundation, whereas all native species except Murray cod were recorded during all inundation periods (Figure 4(c)). The proportion of non-native to native species throughout the study period was always low, ranging from 0% to 5.6%.

In the Murray River, fish CPUE abundance (boat electrofishing) was relatively high in November 2006, increased sharply in March 2010, and was still relatively high in March 2011 at high flows (Figure 4(d)), with Australian smelt, carp gudgeon, and common carp being the most frequently occurring species on each of those sampling events, respectively (Figure 4(e)). Silver perch and Murray cod were only recorded at low flows, and oriental weatherloach only at high flows (Figure 4(f)). Throughout the study period, non-native species ranged in proportion from 8.2% to 58.3%, hence always considerably higher than in Hattah Lakes.

At Hattah Lakes, CPUE abundance of the large- and small-bodied species and of common carp was significantly higher during natural inundation compared with the two managed inundation periods, which were not significantly different from one another (Table 3). Species richness also was significantly higher during natural compared with managed inundation (both periods), and this was also true when native and non-native species were considered separately (Table 3).

Within-system spawning and recruitment

In 2007–2008 and 2008–2009, as an indication of within-system recruitment, YOY goldfish (as well as one common carp in 2007–2008) were recorded among the large-bodied species, and YOY carp gudgeon, flathead gudgeon and Australian smelt among the small-bodied species. YOY golden perch were instead recorded in 2005–2006 and 2006–2007, and later in 2010–2011, goldfish also in 2006–2007 and 2010–2011, and common carp in 2010–2011. YOY carp gudgeon were also present in all other breeding seasons, similar to flathead gudgeon (except in 2008–2009) and Australian smelt (except in 2010–2011).

DISCUSSION

Managed inundation as a 'filter'

In Hattah Lakes, development of a diverse native fish assemblage occurred as a result of pumping, especially during the extended first managed inundation period. A proportion of small-sized fish

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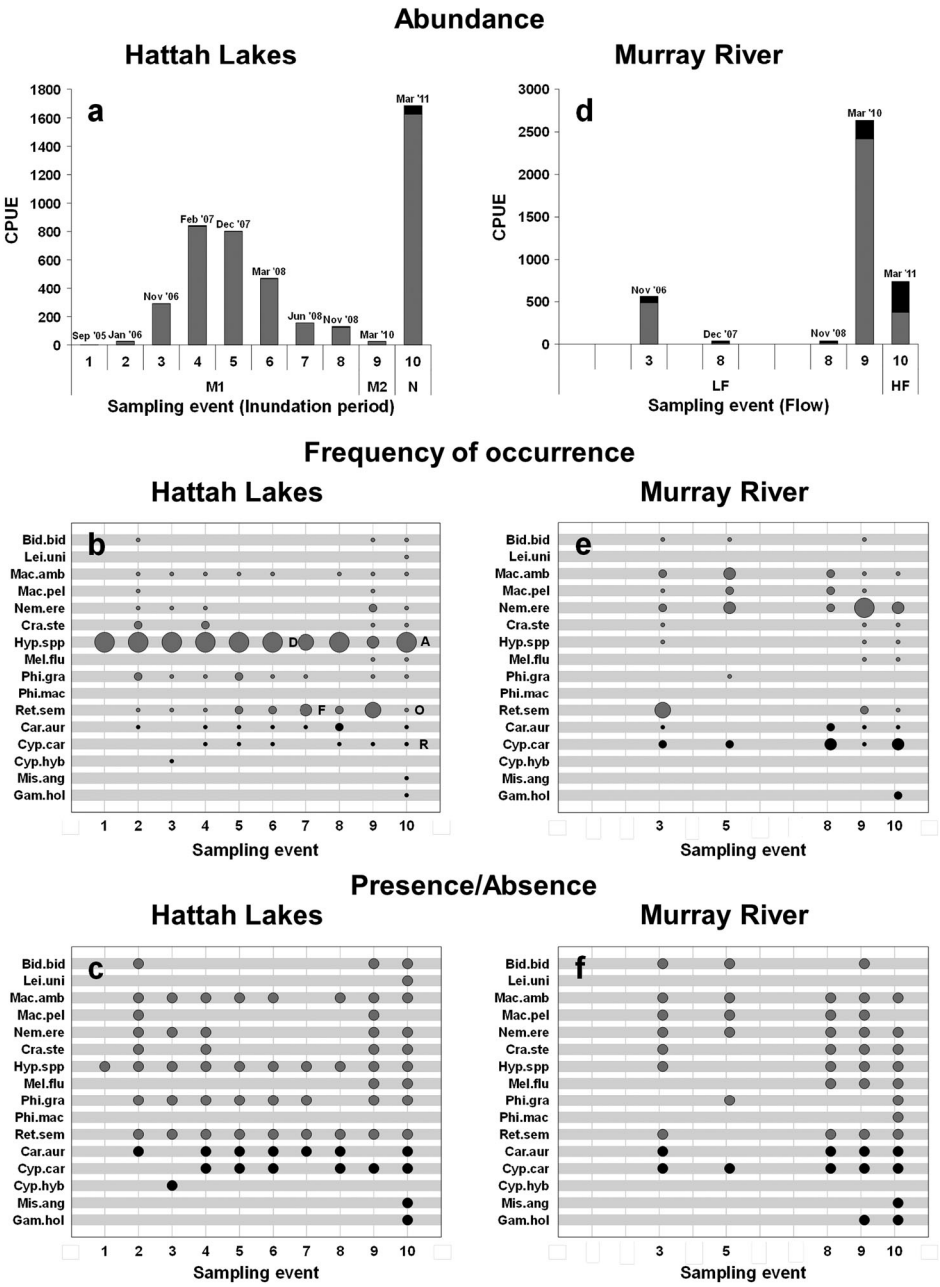

Figure 4. (a) CPUE fish abundance (fish h^{-1}: large and small fyke nets) at Hattah Lakes during 10 events and within three inundation periods from 2005 to 2011. Grey bars: native species; black bars: non-native species. M1 = Managed I; M2 = Managed II; N = Natural (cf. Figure 3). (b) Frequency of occurrence of all fish species (total number of fish) at Hattah Lakes. Grey bubbles: native; black bubbles: non-native (cf. Table 1). Bubble size proportional to frequency of occurrence (relative to sampling event): D = Dominant (> 75%); A = Abundant (51–75%); F = Frequent (26–50%); O = Occasional (6–25%); R = Rare (1–5%). Species abbreviations as in Table 2. (c) Presence/absence of all fish species (total number of fish) at Hattah Lakes. Bubble shading as above. Species abbreviations as in Table 2. (d) CPUE fish abundance (fish h^{-1}: boat electrofishing) in the Murray River during five events from 2006 to 2011. Bars as above. LF = Low flow; HF = High flow. (e) Frequency of occurrence of all fish species (total number of fish) in the Murray River. Bubble plot features as above. Species abbreviations as in Table 2. (f) Presence/absence of all fish species (total number of fish) in the Murray River. Bubble shading as above. Species abbreviations as in Table 2.

entrained in water pumped from the main river channel survived passage through pumps, and sequential pumping events were of additional benefit to the established fish assemblage by providing further immigration from the river and ultimately enhancing spawning and recruitment (Bunn *et al*., 2006).

An investigation of the mechanical effects of irrigation pumps on riverine fish in the Namoi River, Australia (Baumgartner *et al*., 2009), pointed to overall high survival rates (> 80%) for the majority of the species examined, many of which were recorded at Hattah Lakes. However, the absence of eastern mosquitofish during managed

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Table 3. Differences in abundance (CPUE as fish h^{-1} sampled with large and small fyke nets: cf. Table 1) and richness (= sum of species) of the fish recorded in Hattah Lakes during three inundation periods. For abundance, sampling events are: 3 (Managed I), 9 (Managed II) and 10 (Natural) for Chalka Creek, Little Hattah and Lockie; for richness, all sampling events and water bodies are included (cf. Figure 3). Statistically significant effects and *a posteriori* pair-wise comparisons for PERANOVA are at $\alpha = 0.05$ (in bold). $F^{\#}$ = permutational *F*-value

Source	df	MS	$F^{\#}/t$	*P*
Abundance				
Large-bodied				
Inundation	2	7.11	16.00	< **0.001**$^{\#}$
Managed I vs Managed II			1.34	0.235$^{\#}$
Managed I vs Natural			6.04	< **0.001**$^{\#}$
Managed II vs Natural			3.45	**0.003**$^{\#}$
Residual	22	0.44		
Small-bodied				
Inundation	2	2.25	2.54	< **0.018**$^{\#}$
Managed I vs Managed II			1.03	0.300$^{\#}$
Managed I vs Natural			1.59	**0.049**$^{\#}$
Managed II vs Natural			1.60	< **0.043**$^{\#}$
Residual	22	0.89		
Common carp				
Inundation	2	8.19	23.68	< **0.001**$^{\#}$
Managed I vs Managed II			1.00	0.340^{MC}
Managed I vs Natural			4.89	**0.001**$^{\#}$
Managed II vs Natural			4.86	< **0.001**$^{\#}$
Residual	22	0.34		
Richness				
All species				
Inundation	2	4.84	8.81	**0.002**$^{\#}$
Managed I vs Managed II			1.32	0.206^{MC}
Managed I vs Natural			5.21	< **0.001**^{MC}
Managed II vs Natural			3.31	**0.013**^{MC}
Residual	17	0.55		
Native				
Inundation	2	4.06	6.35	**0.009**$^{\#}$
Managed I vs Managed II			1.63	0.121^{MC}
Managed I vs Natural			2.76	**0.016**^{MC}
Managed II vs Natural			3.40	**0.011**^{MC}
Residual	17	0.64		
Non-native				
Inundation	2	5.07	9.71	< **0.003**$^{\#}$
Managed I vs Managed II			0.46	0.647^{MC}
Managed I vs Natural			9.07	< **0.001**^{MC}
Managed II vs Natural			2.98	< **0.019**^{MC}
Residual	17	0.52		

$^{\#}$Permutational *P*-value.
^{MC}Monte Carlo *P*-value (best for small sample sizes).

inundation may be attributable to the position of the pump off-takes and the habitat preference of this species, which has been reported to be littoral (Pyke, 2005; King and Warburton, 2007). In contrast, the absence of oriental weatherloach during managed inundation may result from the recent expansion in range of this non-native species (Keller and Lake, 2007). No conclusions can be drawn with regard to spangled perch, which, although reported as being the only species killed by passage through small-volume pumps (Baumgartner *et al.*, 2009), was recorded in the present study as only one individual during natural inundation – the first known record of this species in Victorian waters (Lintermans, 2007).

Overall, managed inundation by pumping appears to have screened the fish assemblage. However, this was probably not only a result of the 1+ juveniles and/or adults of the large-bodied species being effectively excluded by the pumps but also of the concomitant absence or low numbers in the adjacent Murray River of the small size classes/early life history intervals (≤ 100 mm SL) of some species otherwise known to be abundant in the MDB. Thus, the absence of common carp during the first three sampling events (2005–2006 and 2006–2007 breeding seasons) could have reflected actual overall low abundances of its larvae/early juveniles in the adjacent Murray River. Adult common carp are known to exploit shallow, heavily vegetated backwaters and floodplain areas of the Murray River as spawning and nursery grounds during spring and summer (Smith and Walker, 2004). The young-of-year (YOY) then actively leave these areas to enter the main channel and drift downstream until they reach a size > 50 mm FL (≅ 45.3 mm SL) that allows them to swim actively against the water current and disperse (Stuart and Jones, 2006). Given that the highest densities of YOY common carp are likely to be reached in such reproductive 'hot-spots' along the Murray River main channel, the lack of such areas in the vicinity of Hattah Lakes could help to explain the above absence of common carp. This is even more relevant as the second pumping event occurred from September to December 2005, hence spanning the species' reproductive season (Smith and Walker, 2004). Thus, if present in the main channel, YOY individuals below the critical size could have entered the wetland system through the pumps, but this was not the case. Notably, year-to-year variation in recruitment of common carp with particularly strong year-classes in certain years has been reported in the MDB (Brown *et al.*, 2005) and their occurrence is thought to be linked to the availability of exploitable large areas of unstable habitat subject to hot and dry conditions (Bajer and Sorensen, 2009).

The findings of this study suggest that suitable conditions may have to become established in Hattah Lakes for full development of a 'filtered' fish assemblage within approximately 2 years, in line with findings for a constructed wetland in east-central Florida (Langston and Kent, 1997). Because the most abundant small-bodied species in Hattah Lakes showed similar levels of within-system recruitment in 2006–2007 and 2007–2008 (see section 'Spawning and recruitment'), factors linked to assemblage-level population dynamics may have contributed to the shaping of the fish

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assemblage (Metzker and Mitsch, 1997; DeAngelis *et al.*, 2005; Bond *et al.*, 2010). Among the abiotic factors, initial high levels of leachate from inundated plant material and low oxygen may have limited habitat availability (Gehrke, 1992; Kingsford, 2000), acting as an environmental stressor for fish survival (Gehrke *et al.*, 1993; Townsend and Edwards, 2003; Morrongiello *et al.*, 2011). However, more research is needed to determine the tolerance levels of the early life-history intervals of the native (small-bodied) fish species, which may be lower than those observed for their adults (McMaster and Bond, 2008).

The progressive decrease in the relative abundance of carp gudgeon, flathead gudgeon and Australian smelt in Hattah Lakes from early 2008 onwards is most likely attributable to increased predation rates by waterbirds but also to deteriorating water quality conditions as the lakes began to dry. In this respect, an aerial survey in November 2007 recorded a mean of 16 097 individual waterbirds from 23 species (Kingsford and Porter, 2009). Whereas, water quality may have affected native fish survival through: (i) increased levels of turbidity due to higher susceptibility of lake sediments to re-suspension from wind and wave action; (ii) an increase in electrical conductivity as dissolved salts became more concentrated in the remaining surface water; and (iii) reduced levels of dissolved oxygen – even though Australian smelt and carp gudgeon (and, possibly, other small-bodied native species) are known to tolerate mild levels of hypoxia as an adaptation to drought conditions (McNeil and Closs, 2007).

Contrary to the native small-bodied species, the higher occurrence of non-native goldfish and common carp towards the end of the first managed inundation period can be explained both by the higher tolerances of these two species to poor water quality and elevated salinities (Balon, 2006) and by common carp growing to larger sizes, hence becoming less susceptible to avian predators (Kloskowsky, 2011). Also, the presence of common carp × goldfish hybrids should be further monitored in the light of recent findings on introgression between these two invasive species that may pose a risk for increased genetic diversity, including adaptation to new environments and potential for spread (Haynes *et al.*, 2011), as well as resistance to hypoxia (Balashov and Recoubratsky, 2011).

Natural inundation and connectivity

The overall increase in fish abundance and species richness during 'natural' overbank flooding (that is, intrinsically constrained by historical regulation) was in line with expectations that full (i.e. two-way) riverscape–floodscape connectivity (Thorp *et al.*, 2008) as opposed to managed (one-way) filling through pumps would allow unimpeded access of fish to wetland resources (Galat *et al.*, 1998). This was evidenced by the overall 'homogenization' in fish assemblage structure across the main channel and Hattah Lakes. However, other factors acting at different temporal and spatial scales (e.g. migration and diel movements) may also have affected fish use of temporary waters (e.g. Cucherousset *et al.*, 2007; Nunn *et al.*, 2007).

Unimpeded access of fish to Hattah Lakes during natural inundation was clearly beneficial to species of conservation significance such as silver perch and golden perch. The resulting two-way level of connectivity provided not only a colonization pathway to the floodplain but also a return pathway to the main channel that was not available during managed inundation. This point is emphasized in that there was no evidence of within-system spawning during managed inundation for these two species (see below). Furthermore, those golden perch, silver perch and Murray cod that colonized the wetlands during the first managed inundation period, while progressing through to adult sizes, perished when the water bodies dried by early 2009. On the other hand, increased levels of connectivity during natural inundation promoted recruitment of non-native species including oriental weatherloach, eastern mosquitofish and common carp. As regards the latter species, measures of control (i.e. removal programmes) may then have to be considered following disconnection of Hattah Lakes after natural inundation (Pinto *et al.*, 2005).

Spawning and recruitment

Generally regarded a 'flood recruitment specialist' (Harris and Gehrke, 1994), golden perch has recently been shown to have a more flexible breeding strategy than previously thought, with evidence of spawning and recruitment under both flood and non-flood conditions as well as throughout the year (Mallen-Cooper and Stuart, 2003, King *et al.*, 2005, 2009; Balcombe *et al.*, 2006; Roberts *et al.*, 2008; Ebner *et al.*, 2009). In this study, no evidence was found for golden perch

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spawning at Hattah Lakes after inundation; rather, those individuals collected were considered to have colonized the system as either drifting eggs or larvae from the main river channel. Lack of two-way connectivity during managed inundation and/or limited resource availability due to recently established biota in the inundated water bodies may have acted as constraints for successful reproduction.

With the exception of a single 85 mm SL common carp in 2007–2008 (Gawne and Scholz, 2006), probably a YOY individual but whose size may also fall within the range of 1-year olds (cf. Vilizzi and Walker, 1999), the lack of within-system recruitment for this invasive species is at first sight remarkable in view of its high adaptability and potential for spread in Australian waters (Koehn, 2004). However, lack of recruitment could simply be explained by the absence of ripe females. Female common carp are known to reach maturity at a median age of 2.7 years and 328 mm fork length (FL; ≅ 300 mm SL) compared with 1.1 years and 307 mm FL (≅ 281 mm SL) for the males (Brown *et al.*, 2005). Thus, even though within the course of the present study maturity would have been reached in the 2008–2009 season (SL range: 305–555 mm), deteriorating water quality conditions may have limited spawning and/or survival of the free embryos and larvae of common carp (Balon, 1995). Conversely, within-system recruitment was evident for goldfish, and this agrees with the reported age at maturity for this species between 1 and 2 years under climate conditions comparable with those of the study area (Lorenzoni *et al.*, 2007).

Successful within-system recruitment of carp gudgeon, flathead gudgeon and Australian smelt indicates that inundated water bodies of Hattah Lakes provided suitable conditions for reproduction. However, the likely presence in the MDB of distinct taxa making up the carp gudgeon group *Hypseleotris* spp. (Bertozzi *et al.*, 2000) may have masked asynchronies in taxon-specific reproductive events.

Rehabilitation versus restoration for native fish conservation

Rehabilitation and restoration projects for river–floodplain ecosystems are long-term undertakings that must focus on the dynamic interplay between main channel, floodplain and tributaries (Buijse *et al.*, 2002). Historic intervention measures at Hattah Lakes in response to river regulation (Walker, 2006) have addressed this dynamic interplay from different perspectives, ultimately affecting conservation efforts. According to Aronson *et al.* (1993): (i) restoration *sensu stricto* is the (near-)complete return of a degraded ecosystem to a pre-existing state; (ii) restoration *sensu lato* is the re-direction in a trajectory resembling the one presumed to have prevailed before disturbance; and (iii) rehabilitation is the resumption of damaged or blocked ecosystem functions with the objective to raise ecosystem productivity. Also, unlike restoration *sensu stricto* that seeks a complete return to the historic ecosystem, both restoration *sensu lato* and rehabilitation may settle on one of several alternative steady states.

In the case of Hattah Lakes, neither hydraulic modifications nor intervention through pumping can be regarded as restoration *sensu stricto* measures, both being constrained by historic river regulation. Instead, hydraulic modifications, by lowering the critical CTFT and extending flood water retention time while maintaining two-way connectivity with the main channel, are to be regarded as a means of restoration *sensu lato*; conversely, managed inundation by pumping, which provides one-way connectivity to the wetland system, is to be considered a measure for rehabilitation. In this study, the outcomes of both approaches to the 'reintegration of fragmented landscapes' (Aronson *et al.*, 1993) on the structure of the fish assemblages were clearly different, and involved a trade-off between development of a filtered fish assemblage, which was dominated by native small-bodied species and relatively devoid of non-native species (at least within the duration of the first managed inundation period), and a more diverse one through natural inundation, comprising also native large-bodied along with some less common species, but at the cost of a larger number of non-natives.

A major impediment to rehabilitation of Hattah Lakes by hydraulic intervention through pumping was the complete drying of the water bodies by early 2009 because of to low river flows and cessation of the pumping operations. This caused the complete disappearance of the fish assemblage owing to lack of connections back to the main channel, which were instead present during natural inundation. If pumping is to represent a viable rehabilitation option for fish conservation at Hattah Lakes (e.g. in a filtered 'steady state', as documented in this study), then water allocation measures through pumping should be

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implemented to guarantee the maintenance of one or more refuge water pools through dry conditions in at least part of the system until the next (natural or managed) inundation event. During periods of overbank flooding, this would provide opportunities for lateral movement of fish from Hattah Lakes to the Murray River, where these fish can contribute to regional fish populations.

The continuing, long-term monitoring of Hattah Lakes represents a key component of the integrated wetland conservation framework recently adopted by the Ramsar Convention (Finlayson, 2003). The information collected throughout this study will contribute knowledge on the conservation values of semi-arid wetlands as part of a wider mosaic of areas of biodiversity in low-rainfall regions as well as on the extent of impacts of human activities on such areas, including options for mitigation and rehabilitation (Williams, 1999).

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